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Effects of storm-induced sand scour on *Patella vulgata* off south-west Britain

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Abstract

This study investigates the impacts of storm-induced sand-scour on common limpets (*Patella vulgata*) off south-west Britain, focussing particularly on the physical impacts of this process, as well as shore recovery. Unusually polished limpets were found living on a rocky shore (Westcombe Beach, South Devon) following a series of large storms that occurred from December 2013 to mid-February 2014. The extent of the storms was completely unprecedented, and it was one of the most exceptional periods of winter rainfall in England in at least 248 years when records began. It was clear that the limpets and surrounding epilithic communities at Westcombe Beach had been abraded by suspended particles in the storm waves. Limpets on an exposed shore and a sheltered shore were investigated by means of shell measurements and compression tests to determine differences in thickness and strength in months following the storms. Photoquadrats were taken on the storm-exposed shore to monitor living limpet clusters and associated communities. Sand-scoured shells were significantly thinner for their size than non-scoured shells, but these increased in thickness as time passed after the storms. Sand-scour did not influence shell strength between the two sites, though sand-scoured shells characteristically flaked and crumbled under compressive force. It was surprising to find that sand-scoured limpets were able to repair their periostracum on the uppermost parts of their shell, although the mechanisms for doing this are not known. Given that global climate change is expected to increase coastal storms, these findings shed light on the likely impacts of increased sand-scour on exposed shores.

Keywords

Patella vulgata, limpet, storm, sand-scour, rocky shore, shore recovery, periostracum.

Introduction

Climate change is now established as a scientific certainty and a phenomenon which will have impacts, yet predicting those impacts is a challenge. It is driven by rising concentrations of greenhouse gases (primarily CO₂) building up in the atmosphere, warming the oceans as a result. The Fifth Assessment (AR5, 2014) by the Intergovernmental Panel on Climate Change (IPCC) reported an average rise in global sea surface temperatures of 0.74°C between 1906 and 2005, with recent indications of a rapid temperature increase in the ocean's upper 2000m since 2005 (Llovel *et al.* 2014). It is clear that this anthropogenic climate change threatens to alter coastal marine ecosystems and their services. One major source for concern is the increased occurrence of severe storm events. The UK Met Office expects an increased intensity of Atlantic storms, predicting that long-term warming of the sub-tropical Atlantic will enhance the amount of moisture in storms taking a southerly track. As storms feed off latent heat, warmer waters provide them with increased energy. The Center for Climate and Energy Solutions (C2ES, 2007) reported that tropical storm frequency in the North Atlantic (since 1996) has exceeded the maximum of the 1950s by 40%.

From December to February 2013/14, a number of storm surges hit the UK. The UK Met Office declared that it was the wettest winter in 250 years, with eight storms recorded at Plymouth Coastal Observatory's wave buoys during that time. These extreme events were linked to persistent perturbations to the jet stream over the Pacific Ocean and North America. The North Atlantic jet stream steers weather systems towards the UK, providing ideal atmospheric conditions in which depressions can form: in December and January 2013/14, a particularly active sequence of depressions strengthened the jet stream which led to the extreme weather conditions (Met Office). Varied research is now underway in SW Britain to determine the physical impacts of these storms – Inch *et al.*, for example, were awarded a £50,000 emergency grant from the Natural Environment Research Council to establish directional movement of sediment in the storms. But, whilst the physical and human impacts of major storms are well-studied, the ecological implications are less well known (Harris *et al.* 2011).

Major storms can, and often do, lead to high mortalities in marine biotic communities, both in intertidal and benthic habitats (Harley *et al.* 2006). For example, a storm at Lonafjörður in Iceland (2006) eradicated the rich *Arctica islandica* bivalve population from their soft-bottom habitat to the extent that no recovery is predicted (Thórarinsdóttir *et al.* 2009). In intertidal habitats there is extensive evidence of storm damage to larger organisms, such as macroalgae, which are easy to access and study. However, smaller organisms such as gastropod molluscs are more easily overlooked, and 'damage' is generally measured as total loss of these organisms from the shore. Guiler (1974) observed widespread loss of *Durvillaea* (algae) from Tasmanian shores following an intense storm, as well as noting the obliteration of nearly all patelliforms. The study used presence and absence as a proxy for patelliform 'damage', as well as further stating that individuals living in clefts and cracks on the shore did not 'suffer', simply because they were still present. It is likely, however, that even the individuals that were still present post-storm were 'damaged' on another level.

The limpet *Patella vulgata* is a microphagous grazer found in the mid-intertidal zone of nearly all rocky shores in SW Britain. These limpets play an important role in

community structuring on exposed rocky shores, by means of regulating macroalgal recruitment through consumption of early stages (Jenkins *et al.* 1999). Wave exposure is a major player in determining *P. vulgata* distribution, and population densities tend to decrease as wave shelter increases (Thompson 1980). However, it is under question whether wave exposure and its effects could have negative community impacts as storm frequency increases. The present study arose through conversations with ecologist Dr Richard Kirby of the Marine Biological Association, who noticed sand-blasted shores at Westcombe Beach in Devon, a site he visits regularly, following the 2013/14 winter storms. This is an exposed rocky shore with a high abundance of algae and limpets. It bore the brunt of waves from multiple storms as it was exposed to the strong prevailing winds. In mid-February 2014, after the extreme weather, limpets in the intertidal zone were polished by the storms and most associated epilithic biota had been removed, leaving unusually glossy yellow-shelled limpets on barren rocky outcrops. It was apparent that the leathery outermost layer of these limpets, the periostracum, had been completely abraded off. This raises concerns as the periostracum is assumed to play a number of important roles, for example in shell growth (Taylor *et al.* 1969) and predation protection.

This unusual occurrence was clearly due to sand-scour, whereby particles suspended in waves are pounded against the rocks and cause abrasion. Only some studies have investigated the organismal impacts of sand-scour, such as at Ningo, Ghana, where the limpet *Patella safiana*, which is usually common on Ghanaian shores, is absent due to intense shore modification by this process (Evans *et al.* 1993). Shell erosion (e.g. by grazing; Day *et al.* 2000) is considered to be a continual process for which its effects in the short-term are probably slight. However, this case presents a long-term scenario where an increase in storm intensity and frequency may impact shells rapidly by means of sand-scour. Whilst a number of studies have focused on post-mortem sand-scour damage, such as shell thinning (Cadée 1999), there is now an opportunity to investigate the impacts of this on live organisms.

The aim of the present paper is to assess the ecological impacts of the 2013/14 winter storms on patellid limpets and associated species, with particular focus on the effects of sand-scour. Such findings will enable predictions to be made about the future of intertidal limpet communities that may be faced with increased disturbance from storm activity. The hypotheses being tested propose that: (i) limpets on a shore exposed to the 2013-14 storms will have thinner shells for their size than those on storm-sheltered shores; (ii) sand-scoured patellid shells will be weaker than those that are not abraded (with implications for vulnerability to predators); and (iii) the sand-scoured shore will become recolonised as time passes after the storms. Westcombe Beach is the storm-exposed shore (SES) and Eastern King's is the storm-sheltered shore (SSS).

Methodology

Sampling was carried out at Westcombe Beach (50° 17.769' N 3° 55.038' W), an exposed rocky shore in South Devon, and Eastern Kings (50° 21.678' N 4° 09.602' W), a rocky shore in the Plymouth Sound, of which the storms had a far lesser impact due to protection from the Sound and Drakes Island (Figure 1). Both beaches provide a habitat for an abundance of *Patella vulgata*, which were identified to the species level based on shell and foot characteristics, according to identification

guides (Hayward & Ryland 1995). Eastern Kings provided a comparative site to observe the impacts of the storms at Westcombe Beach.

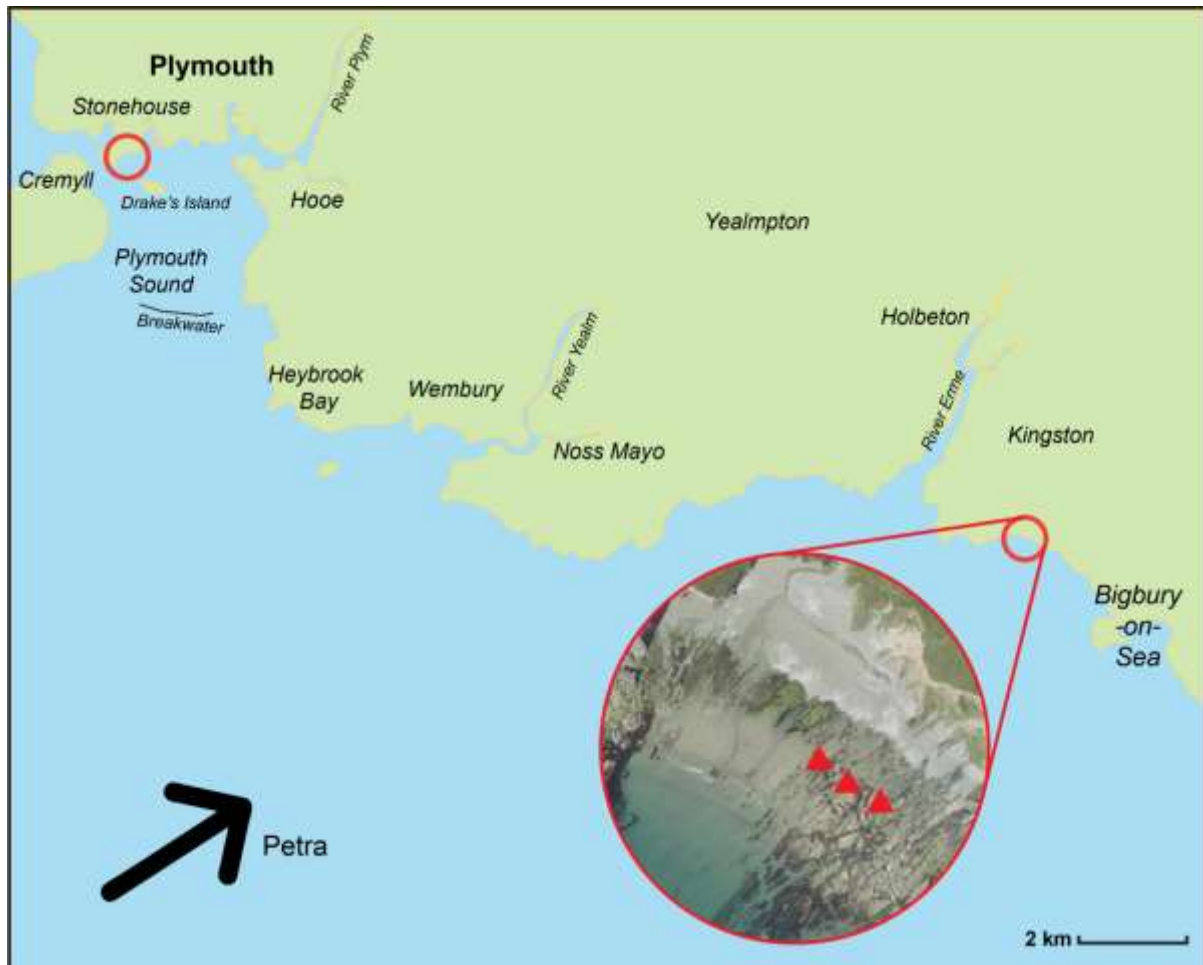


Figure 1: Small red circles ○ indicate Eastern Kings (storm-sheltered rocky shore) in the Plymouth Sound and Westcombe Beach (storm-exposed rocky shore) south of Kingston. ▲ = area sampled at Westcombe. Large black arrow indicates the direction of the storm Petra on 05/02/2014 (*Sevenstones Lightship 67201*).

Shore Recovery

On 15 February 2014, immediately following the winter storms, an initial trip was taken to the SES to assess the impacts of the storms. Twelve haphazard clusters (>4 individuals closely together) of *Patella vulgata* were selected in the mid-littoral zone. Clusters were photographed to record surrounding features to make it possible to locate the same clusters on each visit. In late February, sampling began at the SES. Photoquadrats (PQs; Pech *et al.* 2004) measuring 50 x 50 cm were taken of the marked limpet clusters using a Panasonic Lumix DMC-G1 digital camera, in RAW format for maximum definition and quality. The camera was held at an equal distance (76 cm) from the substratum each time – the distance at which the PQ fitted the shot precisely (Figure 2) – to minimise parallax errors (Pech *et al.* 2004). This distance was maintained using a tape measure. The PQs provide a means of analysing limpet clusters and the associated substratum in order to monitor shore recovery. PQs were taken at low tide to ensure that limpets were fully accessible and

less likely to have left their home scars to feed. Other species within each PQ were identified using appropriate scientific identification guides. Photographs were also taken of individual limpets on a macro setting in order to monitor periostracum recovery. This process was carried out throughout 2014 in February, April, June, September, November, and in January of 2015, in order to see changes over time since the storms.

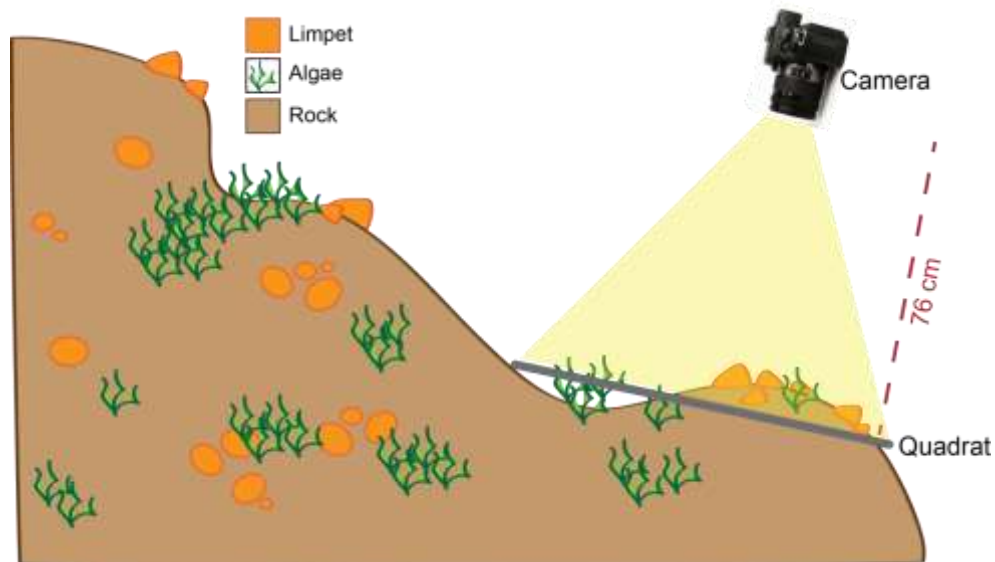


Figure 2: Illustration indicating photoquadrat layout, including photographic technique.

Upon return from the sites, photographs were uploaded onto a computer for close digital analysis. A 100-square grid (Figure 3) was created on *Photoshop CS5.1*, each square representative of 1%. Within each square, 100 equally-spaced dots were placed, with each dot representative of 0.01% of the entire grid. This grid was then digitally placed over each PQ on *Photoshop*, and percentage (%) cover by Algae, Mollusca and Crustacea was determined for each PQ. % cover was estimated following Meese & Tomich (1992), whereby the system is essentially viewed as 2-Dimensional with a maximum possible cover of 100%. For each phylum, the first individual intercepted below a dot was counted and a total % cover worked out. The grid was also placed over photographs of individual limpets to measure % cover of the periostracum. In this case, the number of dots intercepting the shell was counted, and that total divided by 100 to find the percentage value of each dot.

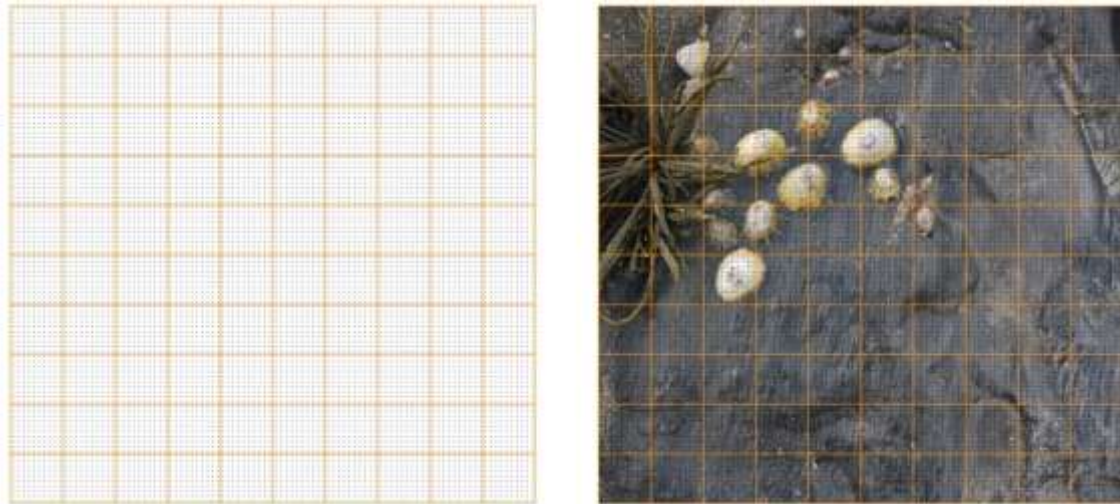


Figure 3: Left: digitally-created % cover count grid, with 100 squares (1% each) and 10,000 dots (0.01% each). Right: grid placed over a PQ ready for % cover estimation.

Shell Parameters

On each trip to the SES, approximately 25 limpets were collected from the lower shore, avoiding those being studied in PQs. Limpets were removed delicately from the rock using a chisel and mallet. All specimens were measured roughly on-site (length, width, height) using a tape measure to ensure they were of similar 'size', a crucial aspect when comparing storm-exposed and storm-sheltered sites. Specimens were stored in plastic Tupperware for transportation. This technique was repeated at the SSS each month within four days of visiting the SES.

Limpets were anaesthetised in a freezer at -20°C for 30 min (Coleman *et al.* 2014), after which soft body tissue was removed using forceps and disposed of appropriately. Shells were left to dry at room temperature. Shell parameters were measured and calculated using formulae for the dimensions of a parabolic cone (Cabral 2007). Shell strength is influenced by a number of shell characteristics (Zuschin *et al.* 2003). Measurements taken for each shell were: length (SL), width (SW) and height (SH) using 6 inch digital Vernier calipers (accurate to ± 0.02 mm); shell base radius (BR) using the formula $(SL+SW)/4$; and shell volume (SV) using the formula $(\pi \times BR^2 \times SH)/2$. Shell volume was the measure for shell 'size', and all tested limpets were considered small ($7,000$ - $15,000$ mm³). Any shells outside of this size range were neglected, as larger shells were generally higher on the shore and are thus indicative of less wave exposure (Hobday 1995).

Shell Thickness

Shell thickness is one of the several proposed anti-predatory morphologies for limpets (Tyler *et al.* 2010). Thickness was calculated for shells from both sampling sites. Eight evenly spaced points were measured, using a small tape measure, around the centre of each shell, midway between the apex and base. These were marked using permanent marker. Then, for each specimen, a thickness reading was taken at each point using digital calipers, which were prepared with a small block of aluminium glued to each jaw (Figure 4) in order to take measurements accurately

around the centre of the shell. By taking eight measurements on each shell, an average shell thickness could be determined.

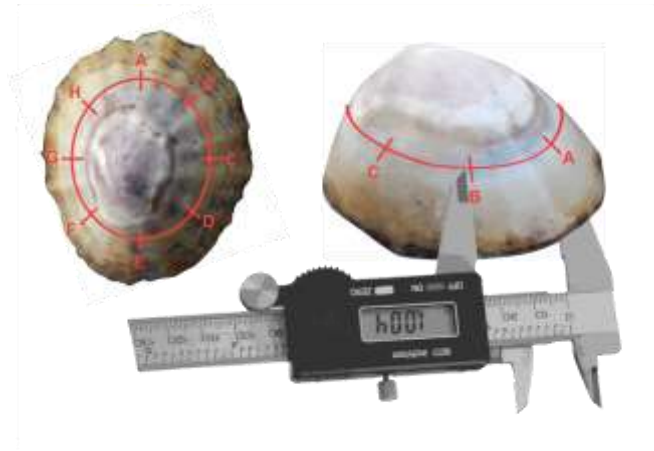


Figure 4: Left: top view of shell with demonstration of how 8 points (A-H) are marked around the centre of the shell – distance between each letter is equal. Right: indication of caliper use at one point. (Not to scale).

Shell Strength

Shell strength can be measured by quantification of the maximum force required to break the shell (Roy *et al.* 1994). Individual shell strengths were measured to determine whether shell thinning by sand-scour is also weakening shells, thus making them more prone to breakage and potentially more vulnerable to crushing predators. This was done using the 1-t compression-testing machine, *Instron* (Coleman *et al.* 2014), which assesses the crushing force that is required to break shells. Each shell is placed flat on a solid platform, and a metal block is lowered slowly (2 mm min^{-1} , 90% sensitivity) to the shell apex. The compressive load (N) is fed to a computer (*Bluehill 2* software) where a multi-specimen line graph is produced, with each crack or fracture event appearing on the line as a sharp drop. Each compression was stopped when the shell was deemed ‘damaged’, generally considered as a crack extending from the apex to the base. When this was not the case, the shell was considered damaged once the compressive load reading decreased continuously.

Statistical analysis

Data for % cover (of both organisms and periostracum), shell thickness, shell strength and number of fracture events were reported as a mean \pm SE. Statistical analyses were conducted using Minitab 17. Comparisons of factors between the two sites and across all tested months were conducted using a nested ANOVA (General Linear Model). Post-hoc analyses (Tukey tests) were carried out to determine specific means that were significantly different from each other. Differences were considered significant at $P < 0.05$. All data sets were tested for normality (Anderson-Darling) and equality of variances (Levene’s).

Results

Shore recovery

Shore recovery was observed between February and September 2014. 'Recovery' was measured as the change in mean % cover of certain groups within each PQ (Foster *et al.* 1990) over time. These groups were Mollusca, Crustacea and Algae. % cover was recorded on visits to the SES in February, April, June, September, November (2014) and January (2015). Of the 15 clusters that were selected for photographing initially, only nine have data from every month as some could not be re-found. Eight clusters showed palpable signs of recovery (i.e. increase in biomass) of one or more phyla, though changes in % cover between months were statistically non-significant. Visually, the settlement of juvenile limpets (*P. vulgata* and *P. depressa*) and juvenile barnacles (*Semibalanus* spp.) within clusters were the clearest indicators of recovery. There were also clear signs of algal recovery on the shore (Plate 1), though this rarely occurred within PQs due probably to grazing by limpets. Following a series of mild storms in November 2014, % cover within PQs was occasionally less compared to data for September, implying a degree of reversal in shore recovery.



Plate 1. Photograph of juvenile algae on previously sand-scoured rocks (November 2014), an indicator of shore recovery. (Photo: Jake Jefford).

One of the most interesting observations made on the SES was a change in limpet shell appearance. Many of the glossy sand-scoured shells that dominated the shore in February 2014 were rougher-textured and darker-coloured by September. This is because the limpets had repaired their periostraca. This phenomenon was visible in most clusters, two of which are shown in Figure 6. Following Meese & Tomich's (1992) 2D dot count method, a periostracum % cover was estimated for certain

individuals. % cover data were then compared between months. For example, the data for Cluster 10 (Figure 5i) are: Specimen **A**, ~84% periostracum 'regrown' from April to September, then 100% loss by November; Specimen **B**, ~92% periostracum 'regrown' from April to September, then 100% loss by November; Specimen **C**, ~55% periostracum 'regrown' from April to September, then 100% loss by November. An interesting observation was that for many limpet shells (e.g. limpet B, Figure 5ii) the periostracum appeared to form near the apex of the shell, despite the fact that mineral deposition occurs at the shell base via the mantle.

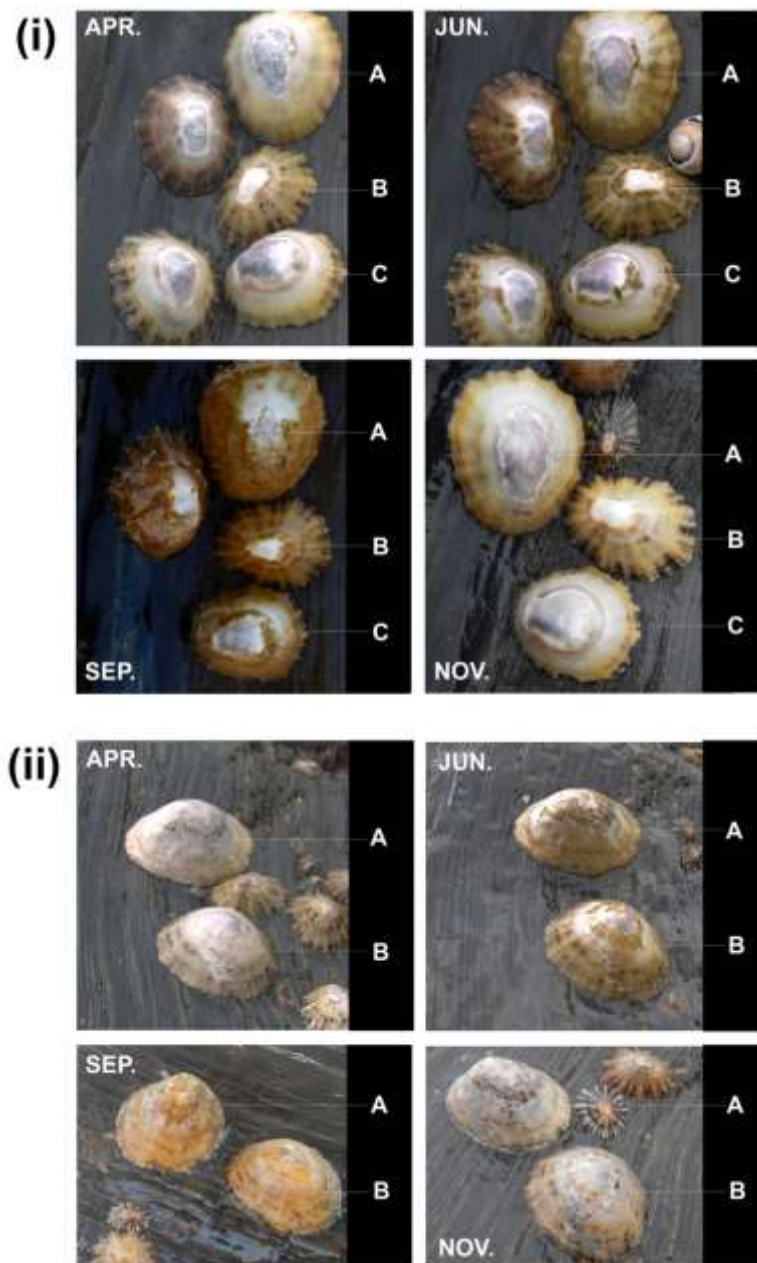


Figure 5: Close-up photographs of the same *Patella* individuals from two clusters from the SES – officially labelled Cluster 10 (i) and Cluster 3 (ii) for experimentation – in April, June, September and November, 2014. Letters **A**, **B** and **C** correspond to the same individuals in each PQ each time. (Photos: Jake Jefford).

Shell Parameters

Shell Thickness

All limpet shell thickness data were normal (Anderson-Darling, $p = 0.291$). In late February, approximately 5 days after the end of the storms, shells were significantly thinner ($p = 0.007$, nested ANOVA) for their size (vol $\sim 10,000 \text{ mm}^3$) at the SES than at the SSS (Figure 6). Shells on the SES ($n = 24$) had a mean thickness of 2.35 mm compared to shells on the SSS ($n = 26$) which had a mean thickness of 2.52 mm. Shells were also significantly thinner between sites in January 2015 ($p = 0.002$). The overall change in thickness over time on the SES was significantly different to that on the SSS ($p = 0.015$). A Tukey test for SES data revealed a significant difference in mean shell thickness between February and September, February and November, and September and January (2015), indicating that shells experienced either noticeable growth or thinning at certain times. For example, an average thickness increase of approximately 0.28 mm occurred from February to September. These differences are clearly correlated with changes in dominant wave height, the proxy for wave action (Figure 6). In contrast, a Tukey test for shells at the SSS indicated no significant change in thickness between any months, as can be seen in Figure 6 where shell thickness remains relatively consistent.

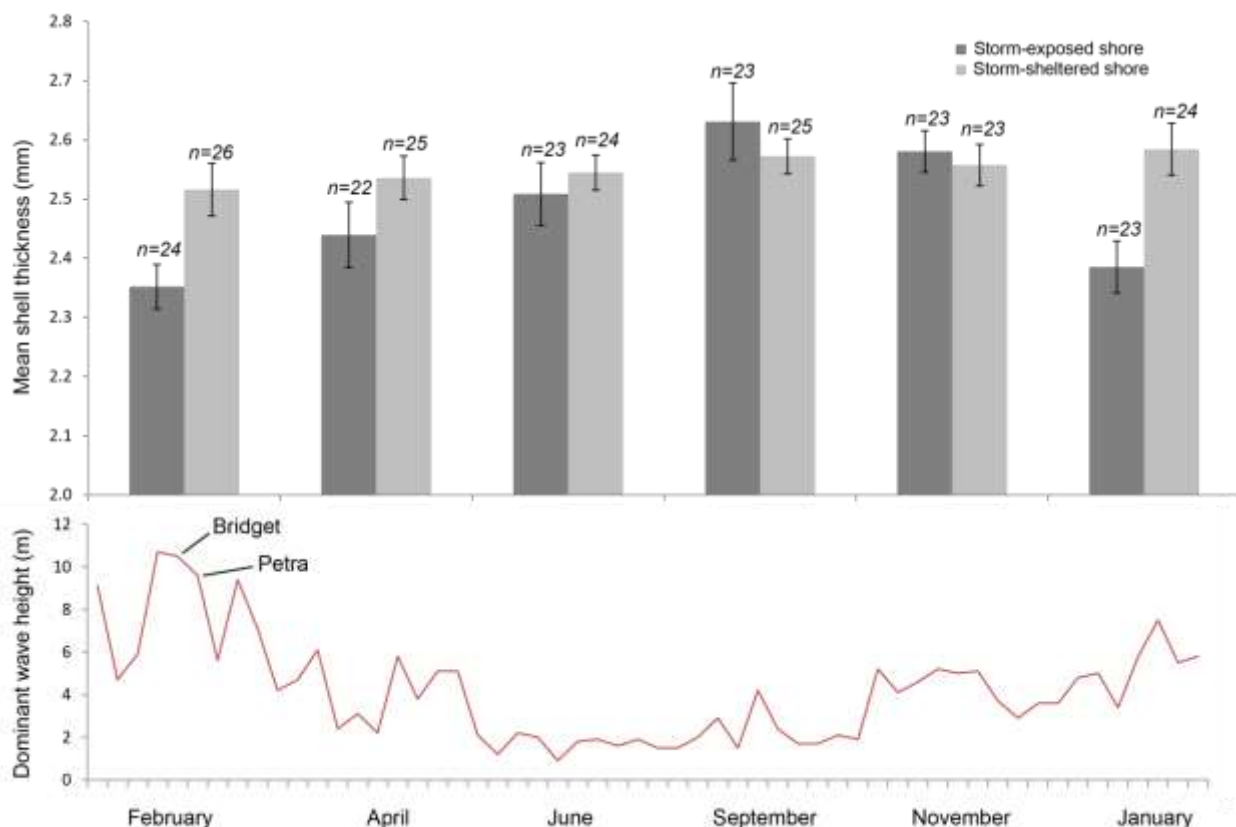


Figure 6: Changes in shell thickness over time for limpets of similar size between a storm-exposed and storm-sheltered rocky shore (mean \pm SE). Red line depicts weekly dominant wave height (*Sevenstones Lightship 62107*) from December 2013 to January 2015, with approximate locations of two major storms (Bridget and Petra) indicated.

Shell Strength

Similarly to results from shell thickness tests, shell strength (N) at the SES appeared to also increase over time until wave activity increased following September (dominant wave height >5 m). The mean strength of sand-scoured shells increased from April to September, and then decreased following the mild storms that occurred in November. Despite a nested ANOVA revealing significant shell strength differences between the two sites during most months, there was no clear pattern in these differences. For instance, shells were significantly thinner at the SSS in February ($p = 0.032$), November ($p = 0.003$) and January ($p = 0.007$), contrary to the hypothesis that shells would be stronger at the SSS. There was no apparent pattern in shell strength changes between the two sites.

Interestingly, though not officially quantifiable, shells on the SES showed a very different response to compression than those on the SSS. There were considerably more fracture events for shells on the SES which were represented as both audible cracking sounds during compression and dips on the digital line graph produced. Whilst storm-sheltered shells tended to break suddenly under compression, often forming a single crack from apex to base (Plate 2i), storm-exposed shells behaved differently. Seven shells (total $n = 18$) crumbled finely at the apex, leaving a large hole (Plate 2ii), and all shells tended to flake in layers. To display these findings, the number of dips (i.e. fracture events) in the line on the line graph was recorded for each shell (Figure 7). An ANOVA revealed a significant difference in the mean number of shell fracture events between shells on the SES and SSS ($p = <0.01$), and a Tukey test revealed that this significant difference occurred between sites in all the tested months in 2014 (February, April, June, September and November).

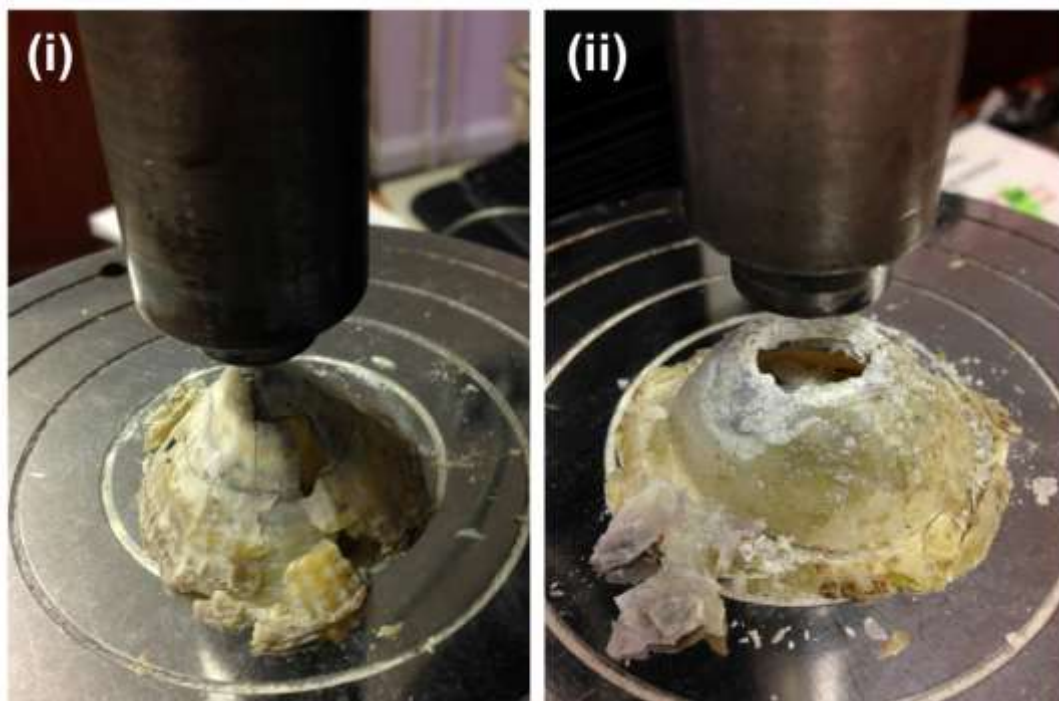


Plate 2: (i) A shell from the SSS with a single crack from apex to base, characteristic of these shells. (ii) A shell from the SES with a hole at the apex and obvious crumbling and flaking of the entire shell. (Photos: Jake Jefford).

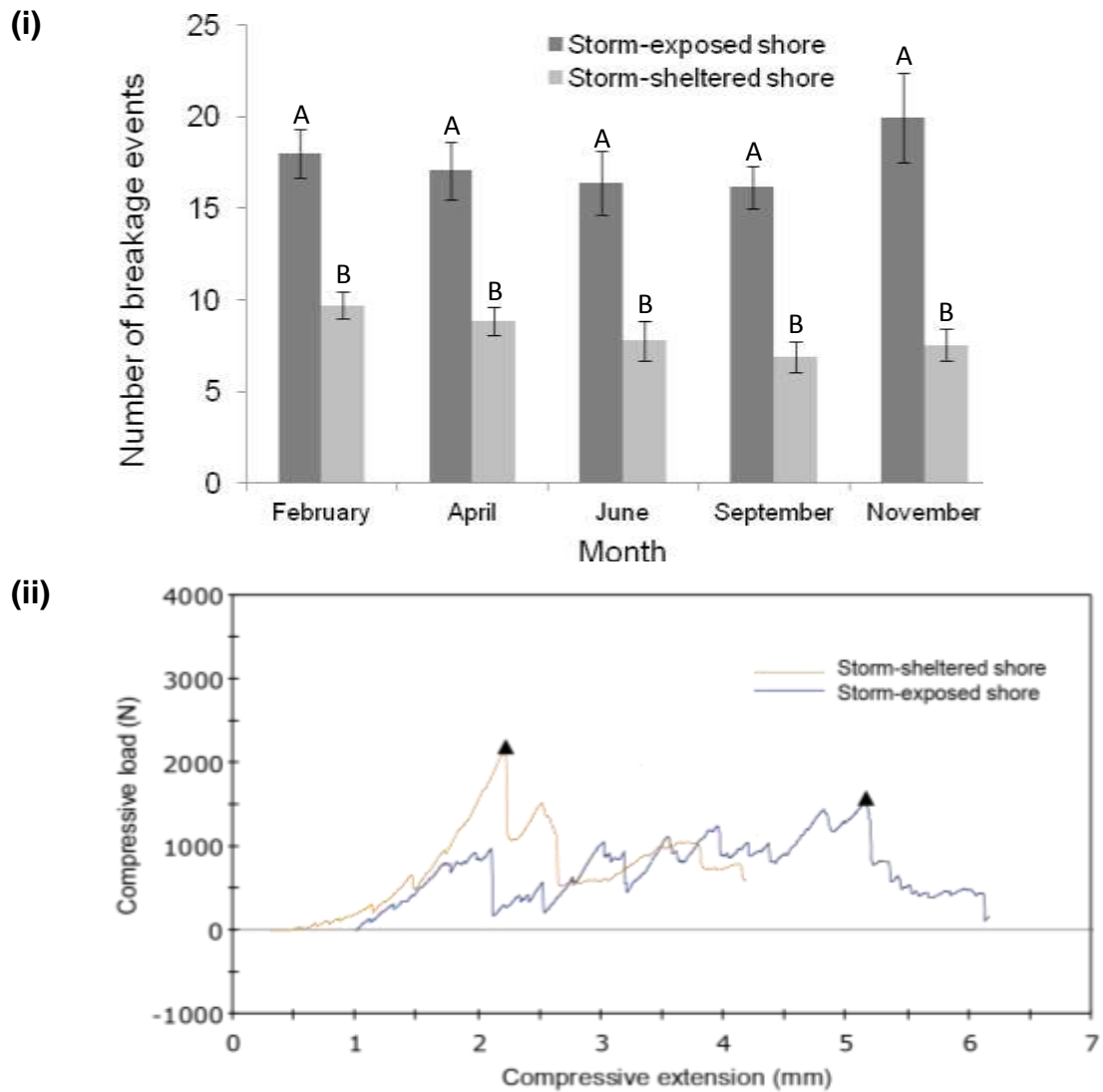


Figure 7: (i) Comparison of number of breakage events between shells on the SES and SSS as time passed since the 2013-14 winter storms (mean \pm SE, $n = 18$). Bars labelled A are significantly different than corresponding bars labelled B (Tukey). **(ii)** Example of two strength lines produced on *Bluehill 2*, demonstrating a high number of fractures (sharp dips, ~18) on the SES compared to few (~5) on the SSS. ▲ = maximum compressive load.

Discussion

Shore recovery

Whilst all PQs included limpets that showed recovery at an individual level, there was no significant evidence to indicate recovery of the shore as an entirety. PQs that were scarce of any organisms (except from limpets) tended to remain that way over the course of 11 months following the 2013-14 storms. This could be a result of extensive damage that will not allow for rapid recolonisation of the rock, or it could be that certain selected rocks were never colonised by other organisms in the first place. Pre-storm data would be necessary to accurately determine this. There was evidence for settlement of juvenile patelliforms and barnacles shortly after the storms, however more time would be needed to monitor their success. In some PQs, novel recruits (as well as adults) were removed following further storm activity in November 2014. This leads to questions about whether an increase in storm frequency and intensity could prevent the settlement of new recruits on exposed shores.

Periostracal Recovery

The limpet shell is the result of a controlled biomineralisation process (Marin & Luquet 2004) which produces several calcium carbonate layers (myostraca). Using electron microscopy, Suzuki *et al.* (2010) confirmed this in the limpet *Lottia kogamogai*. An external proteinaceous layer also exists called the periostracum (Marin & Luquet 2004). This is formed at the shell mantle via the synthesis of precursor macromolecules in the Golgi cisternae, where they fold into structurally ordered units (Saleuddin & Petit 1983; Waite 1983). This process takes place in a groove close to the shell surface which forms where the mantle edge folds (Lowenstam & Weiner 1989), with the periostracum emanating from the mantle and curling up around the shell edge (Clark 1976). The periostracum is believed to provide the limpet with protection from abrasion (here from sand-scour), which has been found to remove fragments of periostracum on older portions of the shell (Clark 1976).

Photograph analysis indicated clear recovery of periostraca. Storm-exposed shells in April were totally polished compared to those on the SSS. After five months, the same individuals appeared to have regenerated this layer. These findings at the SES provide an intriguing insight into the ability of *Patella vulgata* to overcome storm-induced physical damage. If the predicted benefits of periostraca are correct, then an ability to regenerate it is crucial. Without this ability, sand-scoured populations could face increased mortality. For example, these individuals are more prone to environmental damage, both to the shell and soft tissue, which is isolated from the environment by the periostracum (Clark 1976). Additionally, limpet growth takes place at the periostracum – it is thought to provide an initial substratum for mineral deposition at the shell edge (Taylor *et al.* 1969). Suzuki *et al.* (2013) confirmed that the initial formation of calcite crystals (a key component of molluscan hard material) occurs here. Without this layer, growth is reduced, meaning that an individual may not be able to appropriately and efficiently exploit its surroundings. Also, vulnerability to predation may increase: smaller limpets require less force to be removed from substrate by prying predators (Silva *et al.* 2008), and size provides a refuge from crab predation (Vermeij 1976).

Contrary to the findings of Clark (1976), limpets on the SES in this study had lost their periostraca entirely, not just on older sections of the shell. This could be due to the intensity of the storms, though pre-storm information about the state of these shells is needed to determine whether sand-scour was majorly responsible or not. The rate of periostracal regeneration has not been documented. Such information would be useful in determining whether limpets on the SES regenerated their periostraca at a higher rate or expended more energy than those on the SSS, which is possible. Further storm waves in November 2014 once again abraded all the 'recovering' shells. This explains polished shells in January 2015, and could spark future studies into repeated periostracal recovery. Interestingly, whilst it is understood that periostracal growth starts at the mantle, several limpets displayed isolated patches on mid and upper sections of the shell. This suggests the potential ability of these limpets to synthesise organic materials at other parts of the shell, possibly directly targeting areas in need of recovery *through* the myostraca. This phenomenon has not been studied, and is the subject of ongoing investigations (Jefford, 2015).

Shell parameters

Shell Thickness

Shell growth (in size and thickness) occurs when calcite crystals form on the periostracum, and shells become bigger via calcification (Suzuki *et al.* 2013). Over time, increased mineral deposition causes the shell to become thicker. Results of this study show that the myostraca of limpets on the SES were abraded and/or depleted as a result of storm-induced sand-scour, hence the obvious thinning of shells, whilst limpets on the SSS were not. On the SES, a clear pattern (Figure 6) exists between changes in shell thickness over time and local wave activity (*Sevenstones Lightship 62107*). As wave activity died down after the storms, the mean thickness of limpet shells increased accordingly from February to September. The difference in mean thicknesses between months on the SSS was far lower than that for the SES. This implies that storm-sheltered limpets may be investing less energy into biomineralisation processes as their thickness is sufficient to enable survival on a shore where storm-induced stressors are reduced. Thinner shells in February at the SES than the SSS indicate the intense period where shell thickness at the SES was dramatically reduced.

Also, in September, storm-exposed shells were thicker for their size than those on the SSS. It is probable that storm-exposed limpets were investing higher energy into growth, so as to enhance survival under demanding conditions, and were able to surpass storm-sheltered limpets over a short time period. Though this is impressive, past research (e.g. Blundon & Vermeij 1983) indicates that limpet shell repair is energetically costly. If storm frequency is to increase, this energetic cost could be fatal. The ability for limpets on the SES to rapidly increase in thickness is crucial, as they were significantly thinned once again following further storms in November 2014. Had they not recovered, shells may have been thinned until protection of soft tissues was insufficient. It would be useful to monitor limpets on this shore over a long time period, as it may be that they are routinely thinned by sand-scour, and thus have adapted to deal with repeated storm-related stressors. However, the question to consider is whether an increase in storm frequency due to climate change might limit the time that these limpets have to recover, increasing population mortalities.

Thickness differences between the two sites are not assumed to be due to predator cues, as both shores are similar in nature.

Shell Strength

Storm-exposed shells had a higher mean compressive load than storm-sheltered shells in February, November and January (contrary to the hypothesis), despite being thinner. This is probably due to variations in shell morphology between both sites, such as shell shape, that may have influenced where weak spots occur. Also, use of the *Instron* machine to obtain strength measurements for organic material is a novel technique, and these unexpected strength readings may be a result of methodological error. This method should be refined, for example crushing limpets attached to rocks to compensate for uneven shell bases. It was assumed that compression tests would cause each shell to crack fully from the apex to the base because the compression acted directly on apex, and higher compressive load readings were expected for storm-sheltered shells. This was not always the case here, however a larger sample size may have seen different results. Tests clearly showed a difference in the breakage behaviour of shells from the two sites. The thinner storm-exposed shells were seemingly weaker all over, showing a high number of breakage events and extensive flaking of the shell into its component myostraca. This suggests that sand-scour damages and weakens the bonds holding shell units together, creating weak spots throughout the entire shell. In contrast, the low number of breakage events in storm-sheltered shells is likely due to a strong, uniform complex of interlocking molecules that should exist to maintain an evenly resistant shell.

There was no indication that shells became less prone to the observed flaking behaviour over time, implying that an increase in shell thickness does not correspond to an increase in shell strength. Consistency in these means across all months shows that limpets were not able to strengthen their shells at weak spots. The mean number of breakages was higher in January 2015 compared to other months, suggesting that shell layers weakened even further after another storm. It is possible that this weakening will carry on with more storm events. A source for concern is that thinner, weaker shells make limpets more prone to predation. Patellid limpets are consumed by a variety of predators including blennies (Milton 1983) and cancrid crabs (Silva *et al.* 2004). Cancrid crabs attack via apex crushing and marginal crushing. While apex crushing destroys the upper portion of the shell, marginal crushing chips the shell edge and may fracture the shell (Tyler *et al.* 2014). Shells from the SES often demonstrated apex crumbling and multiple shell fractures, so it is probable that they are at risk.

Final Remarks

The results of this study indicate that *Patella vulgata* are able, in some ways, to overcome the physical changes experienced from storm-induced sand-scour. This includes recovery of the periostracum and an increase in shell thickness over time following an extreme storm event. Such findings imply that these limpet populations may continue to be successful and recover from storm-induced damage. However, an increase in storm frequency may not provide limpets with the time they require to overcome and amend the physical damage from previous events. An increase in storm frequency is expected to be rapid, raising concerns about the ability of this

species to evolve and adapt to a changing environment. In addition, the consistent flaking behaviour of sand-scoured shells indicates that, while limpets can repair in thickness, the integrity of the shell structure could be permanently damaged. This has implications for increased vulnerability to predation and environmental stressors, thus affecting survival success. Conservation measures must be taken in future years to ensure the persistence of intertidal limpet populations as abrasion events increase. This species is a key player in the maintenance of rocky shore habitats in the UK, therefore exposed shores should be protected as fully as possible by means of structures and technologies that prevent long-term damage.

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